

1 **Evolutionary Patterns in Limb Length, Microhabitat Use, and Adhesive**
2 **Performance: There's More Than One Way to Climb a Tree**

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Abstract

The study of ecomorphology links microhabitat and morphology, with anole lizards representing a particularly well-studied example. By comparing ecomorphological patterns across lizard clades, we can investigate the repeatability of evolution; revealing the extent to which evolution produces similar solutions in response to particular environmental challenges. Gecko lizards can be rock dwelling, terrestrial, or arboreal, and have adhesive toe pads, similar to independently evolved pads in anoles, making geckos an excellent system to study morphological adaptation. We examined microhabitat use, limb morphology, and adhesive performance in geckos, finding that geckos had microhabitat use preferences (perch height and diameter) convergent with that of anoles with one gecko genus also exhibiting convergent limb lengths. We also found that arboreal geckos had shorter proximal limb segments than rock-dwelling and terrestrial geckos, similar to patterns observed in other lizard groups, such as skinks. Despite these similarities, we observed relatively longer-limbed geckos using narrower perches, distinct from patterns observed in anoles and other lizard groups. In addition, we found geckos, as a group, have shorter relative limb lengths than anoles. As a result, we conclude geckos and anoles have likely adapted to similar microhabitats via different pathways. While convergent functional morphology and microhabitat patterns may occur, distantly related species likely evolve in the context of their own history along unique evolutionary pathways.

Introduction

Ecomorphology is the study of an organism's morphology and performance in the context of its ecology (Wainwright and Reilly 1994). Habitat use often strongly influences morphology, selecting for morphologies that perform best in particular microhabitats (Wainwright and Reilly 1994). Studies of form and function typically look for correlations between morphology, performance, and habitat use, or convergent morphology in similar habitats, to suggest adaptation (Arnold 1983; Losos 1994b; Wainwright and Reilly 1994; Autumn et al. 2002; Melville et al. 2006; Losos 2009; Siström et al. 2012). Lizards have been a classic system used to study morphology, performance, and habitat use. Overall, researchers have described a wide range of patterns linking the locomotion of lizards to morphology, performance, and microhabitat, but these patterns are typically clade-specific. Anoles represent one of the best-studied groups. Specifically, arboreal perch diameter has received a lot of research attention due to its ease of measurement and apparently intuitive biomechanical implications (Losos 2009). Anole species with shorter limbs use narrower perches, presumably due to a trade-off between speed and balance (Losos and Sinervo 1989; Losos 1990b, a; Losos and Irschick 1996; Irschick and Losos 1998; Macrini and Irschick 1998; Calsbeek and Irschick 2007; Jones and Jayne 2012). Similar morphologies have repeatedly evolved in many of the Caribbean anole ecomorphs. In addition, similar perch diameters and limb length relationships have also been described in *Tropidurus* and *Draco* lizards (Kohlsdorf et al. 2001; Ord and Klomp 2014). Studies of chameleons, which also use narrow perches, have found trade-offs between sprint speed and clinging ability (Losos et al. 1993; Fischer et al. 2010).

In addition to investigating perch diameter, many studies have examined other arboreal ecomorphological patterns or compared arboreal lizard species with species using other microhabitats. For example, saxicolous, or rock-dwelling, skinks have longer limbs than terrestrial species (Vitt et al. 1997; Goodman et al. 2008). Arboreal chameleons have larger feet and better gripping abilities compared to terrestrial species (Herrel et al. 2013). Arboreal and terrestrial geckos have different locomotion mechanics (Aerts et al. 2000). Scansorial *Liolaemus* lizards (arboreal or rock dwelling) cling better than generalist and sand-dwelling species, and in this group, clinging is positively correlated with proximal limb

segment length (Tulli et al. 2011). These studies suggest convergence of species using similar microhabitats may be common. Alternatively, other studies have failed to find significant relationships between microhabitat use and morphology. Climbing and terrestrial *Pachydactylus*, *Chondrodactylus*, and *Rhoptropus* geckos differ in limb length, but these patterns are not consistent across species (Johnson et al. 2005). In chameleons, there are no significant relationships among limb lengths, sprint speeds, and microhabitat use (Bickel and Losos 2002; Herrel et al. 2013). Phrynosomatid lizards also lack convergent ecomorphological patterns among terrestrial, arboreal and rock-dwelling species (Miles 1994). A lack of correlations between microhabitat use and morphology may be due to behavioral plasticity, or weak or absent locomotory trade-offs among habitat types (Zaaf and Van Damme 2001; Goodman et al. 2007; Revell et al. 2007; Clemente et al. 2013).

Together, these studies suggest that convergent ecomorphological patterns do not always occur, convergence may be idiosyncratic to particular groups or communities, such as convergence in Caribbean, but not South American anoles (Macrini et al. 2003; Losos 2009). To investigate this idea further, we quantified ecomorphological traits in geckos, focusing on limb lengths, and adhesive performance. Geckos provide an excellent model system in which to study ecomorphology and locomotion because they show extensive morphological and ecological variability, and repeated evolution into similar habitats (Pianka and Huey 1978; Russell 1979; Carillo de Espinoza et al. 1990; Zaaf et al. 1999; Russell 2002; Johnson et al. 2005; Gamble et al. 2008; Higham and Russell 2010; Gamble et al. 2012). Geckos can be terrestrial, arboreal, saxicolous (rock dwelling) or use leaf litter, and have adapted repeatedly to these habitat types. Geckos are also highly variable morphologically, especially in regards to the presence and shape of their adhesive toe pads, allowing us to compare geckos to both padded anoles and other padless lizards (Ruibal and Ernst 1965; Russell 2002; Russell and Higham 2009; Gamble et al. 2012). Toe pads evolved at least three times in lizards (skinks, anoles, and geckos; Ruibal and Ernst 1965; Irschick et al. 1996). It has even been suggested that adhesive pads evolved multiple times within geckos (Russell 1979; Gamble et al. 2012), allowing for comparisons of geckos that never had pads as well as species that have secondarily lost them. Many studies have focused on the biomechanical properties of gecko adhesion (Autumn et al. 2006a; Autumn et al. 2006b; Huber et al. 2007; Pugno and Lepore 2008; Pesika et al. 2009; Yamaguchi et al. 2009; Hagey et al. 2014), but fewer have

considered adhesion in an ecological context (but see Hecht 1952; Huber et al. 2007; Russell and Johnson 2007; Pugno and Lepore 2008; Russell and Higham 2009; Lamb and Bauer 2010; Stark et al. 2012; Russell and Johnson 2014; Collins et al. 2015). In comparison, much work has been done linking anole toe pad morphology with performance and microhabitat (Irschick et al. 1996; Zani 2000; Macrini et al. 2003; Elstrott and Irschick 2004; Crandell et al. 2014). These studies have typically focused on the generation of friction to quantify toe pad performance. We chose to use the angle of toe detachment (TAD) as our measure of toe pad performance. This whole-animal measurement of performance can easily be measured in the field or lab, and has been used to quantify clinging ability in geckos and frogs (Emerson 1991; Autumn et al. 2006a; Moen et al. 2013; Hagey et al. 2014). TAD measures the maximum ratio of adhesive (negative normal force) and shear force (friction) a toe pad can generate. Species with low detachment angles produce less adhesion relative to shear force, requiring more applied force to produce similar levels of adhesion.

Perch angle, defined as a perch's angular incline above horizontal, is also likely an important parameter influencing arboreal locomotion, especially for species with adhesive pads. Perch angle correlates with toe pad size (Bauer et al. 1996; Higham and Russell 2010; Collins et al. 2015) and affects locomotion kinematics and sprint speed in some lizards (Higham and Jayne 2004; Mattingly and Jayne 2004; Spezzano and Jayne 2004; Russell and Higham 2009; Krause and Fischer 2013) but not always (Vanhooydonck and Van Damme 2001). In addition, studies of anoles suggest species with larger toe pads generate more friction (Irschick et al. 1996), and so steeper perches may require more friction to prevent falling, hence selecting for larger toe pads. Toe pad performance may also relate directly to perch angle. As a result, species with low detachment angles, generating less adhesion relative to friction, may not be able to produce enough adhesion to suspend themselves from inverted perches, and hence may be limited to shallower perch angles (Autumn et al. 2006a; Hagey et al. 2014). By contrast, species with higher detachment angles can likely use steep or shallow perch angles.

Here we compare ecomorphological patterns in geckos to relationships described in other lizards, to investigate their generality. We hypothesize that geckos using large diameter perches would have longer limbs than species using narrow perches, as described in anoles, *Tropidurus*, and *Draco* lizards, due to a trade-off in balance and speed during locomotion

(Losos and Sinervo 1989; Losos 1990a, b; Losos and Irschick 1996; Irschick and Losos 1998; Macrini and Irschick 1998; Kohlsdorf et al. 2001; Calsbeek and Irschick 2007; Losos 2009; Jones and Jayne 2012; Ord and Klomp 2014). Generalizing this hypothesis across perch types, we also hypothesize that saxicolous geckos living on large, open rocky surfaces such as boulders or exposed outcrops will likely experience similar locomotor challenges as many arboreal trunk-dwelling species, and have long limbs (Vitt et al. 1997; Goodman et al. 2008), although this pattern is not always observed (Revell et al. 2007). Lastly, we hypothesize that geckos using steeper perches would have longer distal limb segments (combined toe and foot length) assuming species with longer toes will have larger toe pad and generate more friction, which will be most beneficial on steep perches.

Materials

To compare habitat use, morphology, and adhesive performance, we gathered three datasets: microhabitat observations, limb morphology measurements, and toe pad performance measurements of geckos and anoles (Table S.1). Anole microhabitat and morphology data were gathered from published sources (Table S.1; Losos 1990a, 1994a) and personal communication with J. Losos. Gecko habitat use was observed in Queensland, Australia during September and October 2012 (Table S.2). Morphology and performance were quantified using museum specimens (morphology only), captive live specimens, and wild caught specimens from various locations. One species we observed in the field was putatively a new species of *Oedura*, found in western Queensland and the Northern Territory, previously thought to be *Oedura marmorata*. We refer to it as *Oedura sp.* (P. Oliver, pers. comm.; Oliver et al. 2012). Field caught specimens were euthanized using MS-222 (tricaine methanesulfonate; Conroy et al. 2009), formalin-fixed, and prepared as museum specimens. 50 preserved specimens were submitted to the Queensland Museum at the end of the field portion of this project (Table S.2). The remaining 20 lizards were not euthanized and were released at their original point of capture.

Microhabitat Use

We examined microhabitat use in 63 species of anoles and 13 species of geckos (Table S.1; Losos 1990a, 1994a). While in Queensland, Australia, we sampled 70 individual geckos,

captured by hand using headlamps to reflect eyeshine, while they were active, between sunset and midnight. We recorded the perch on which the animal was first sighted using the categories: vegetation, rock, and ground, and calculated the proportion of observations occurring on each substrate for each species. When geckos were observed on vegetation, perch height and diameter were measured at the point of initial observation with a tape measure. Perch angle was recorded for all perches using a digital goniometer (Johnson model #40-6060) with measurements ranging from 0° i.e., a flat surface, 90° representing a vertical surface, and over 90° indicating an inverted surface.

Morphology

Our measurements of gecko morphology comprised 38 species including field caught, captive, and museum specimens. Using a ruler or digital calipers, we quantified snout-to-vent length (SVL), proximal hindlimb length (from inside the hip joint to outside the knee joint), mid hindlimb length (from outside the knee joint to the ankle joint), and distal hindlimb length (from the ankle joint to the tip of longest digit), proximal forelimb length (from the axilla to outside the elbow joint), mid forelimb length (from outside the elbow joint to the wrist joint), and distal forelimb length (from the wrist joint to the tip of longest digit). We summed our proximal-, mid-, and distal-limb length measurements to estimate total fore- and hindlimb lengths for each individual gecko observed. We also obtained similar morphological measurements for 63 species of anoles (pers. comm. J. Losos; Losos 1990a, 1994a).

Performance

Toe pad performance (toe detachment angle) was quantified for 38 species of live captive and wild-caught geckos (Emerson 1991; Autumn et al. 2006a; Hagey et al. 2014). Anole performance was not examined (see Irschick et al. 1996; Macrini et al. 2003; Irschick et al. 2006). In the case of wild-caught specimens, performance was quantified on the day following capture. Live, non-sedated lizards were suspended by a single hind-toe from a glass microscope slide via their natural adhesive properties. During a toe detachment trial, the glass slide was rotated one degree per second. As the glass slide was slowly inverted, the force generated by the animal's toe pad transitioned from mostly shear to a combination of

adhesive and shear forces relative to the glass slide. At the angle of toe detachment, the animals' toe pad cannot generate the required adhesion to support the animal's mass, and the toe detaches from the glass, dropping the lizard onto a cushioned base. To eliminate extraneous variation, we limited our measurements to only the longest rear toe, alternating between left and right hind feet. While geckos rarely hang by a single toe in the wild, the longest rear toe is ecologically important in other lizard groups (Zani 2000; Schulte et al. 2004). Limiting our test to a single toe eliminates confounding force vectors generated by multiple toes pulling in different directions, and inhibits the gecko from voluntarily detaching (Wang et al. 2010). Measuring toe detachment angle of a single toe provided a precise measure of performance with little individual variation among trials, suggesting behavior had little impact on the assay. Our toe detachment assay is also a mass-independent assay: experiments have demonstrated that individuals detach at the same angle regardless of total mass (Autumn et al. 2006a).

Performance in the field was collected using purpose-built equipment (see Supplemental Material) consisting of a Pacific Scientific Powermax 1.8° stepper motor (model #P21NRXB-LNN-NS-00), Vernier dual-range force sensor, Vernier three-axis accelerometer, Vernier sensorDAQ data-acquisition interface, and a Phidget bipolar stepper control board (#1063_1). Operation and data collection used a custom LabVIEW program (2011 version 11.0.1f2, National Instruments, Austin, TX, USA) running on a Gateway LT series netbook (LT2805u). The frame of our toe detachment equipment was custom-built and acted as a lever with a fulcrum in the center, force sensor at one end, and the lizard suspended from the other end (see Supplemental Material; Autumn et al. 2006a; Hagey 2013; Hagey et al. 2014).

To quantify an individual's performance, we fit observed detachment angles of individual lizards to the Weibull distribution, and estimated the distribution's scale parameter with error (Hagey 2013). To calculate species' mean detachment angle, we calculated a weighted average for each species, weighting each individual's estimated detachment angle by one over the standard deviation of that individual's estimated scale parameter (Hagey 2013). We used the above-described, untransformed, weighted species averages in our subsequent analyses.

Analyses

To conduct our analyses, we used R Studio statistical software (RStudio Team 2015; Version 0.98.501). Species mean perch diameter, perch height, limb lengths, and SVL were natural-log transformed, perch angle was not transformed, and our proportional perch-type observations were arcsine square-root transformed to ensure normality before statistical analyses. To calculate species residual, size independent, limb lengths, we extracted the residuals from an SVL-limb length phylogenetic generalized least squares regressions (PGLS) using the APE R package assuming a Brownian motion model of trait evolution (Paradis et al. 2004). We used a phylogenetic tree pruned from the ultrametric phylogeny of Pyron and Burbrink (2013). The residuals from these PGLS model fits were used as our transformed, size-independent limb measurements. Residual limb length was calculated for each set of analyses separately, only including the relevant species for that analysis. When comparing geckos and anoles, we calculated residual limb lengths using geckos and anoles together, as well as residuals for geckos and anoles separately (see Results). Due to discrepancies between our focal species and the species included in our phylogeny, in all of our phylogenetic analyses, we renamed three tips to include observed species (*Pseudothecadactylus lindneri* became *P. australis*, *Afroedura karroica* became *A. loveridgei*, and *Geckolepis maculata* became *Afroedura hawequensis*). After removing non-focal taxa, these reassignments did not affect the topology. We also assumed a similar age of divergence between *Oedura marmorata* and *Oedura sp.* as Pyron and Burbrink (2013) observed between *O. marmorata* and its sister species *O. gemmata*, because Oliver et al. (2012) hypothesized deep divergences within *O. marmorata*, divergences nearly as large as the distance between *O. marmorata* and *O. gemmata*. The Pyron and Burbrink (2013) phylogeny also differed from previously published phylogenies, specifically within the genus *Strophurus* (Sadlier et al. 2005; Brown et al. 2012). We kept the topology from Pyron and Burbrink (2013) and suggest additional sampling to resolve conflicts. To evaluate if morphological, performance, or ecological variables were significantly correlated, we again used PGLS via the caper library in R (Paradis et al. 2004; Orme et al. 2011), estimating Pagel's λ (Pagel 1999) using a maximum likelihood approach. λ was bounded between zero (no phylogenetic relationship in the data) and one (traits evolve under Brownian motion). We used the same phylogenetic tree as above.

Results

We observed a wide variation in perch types used by geckos in Queensland, with some species preferring vegetation (*Amalosia rhombifer*, *Gehyra dubia*, *G. variegata*, *Oedura castelnaui*, *O. marmorata*, *Pseudothecadactylus australis*, *Strophurus ciliaris*, *S. krisalys*, and *S. williamsi*), others preferring rock (*Oedura coggeri* and *Oedura sp*), and still other species using a combination of perch types (*Gehyra robusta* and *Oedura monilis*, Fig. 1).

To compare ecomorphological patterns between geckos and anoles, we first compared perch diameter and height used by our focal gecko species to those used by anole ecomorphs (Fig. 2). *Pseudothecadactylus australis* used large-diameter perches, high above the ground in the canopy, overlapping with the trunk-crown and crown-giant anole ecomorphs, (Fig. 2). Similarly, the habitat use of most *Gehyra* and arboreal *Oedura* species overlapped with the anole trunk-ground ecomorph, as these geckos usually used vertical tree trunks (Fig. 2). On the other hand, *Oedura monilis* and *Gehyra robusta* both differed from observed anole ecomorphs, possibly due to their use of rocks and terrestrial microhabitats in addition to arboreal perches (Fig. 1 and Fig. 2). Lastly, *Strophurus* geckos used narrow perches near the ground, similar to grass-bush anoles, although *Strophurus ciliaris* occurred on perches even lower than those used by grass-bush anoles (Fig. 2).

To further compare geckos and anoles, we calculated residual total limb length combining our gecko and anole data (Fig. 3A). The resulting residual limb lengths were not normally distributed (Shapiro-Wilk normality test, $p < 0.01$, see Fig. 3A inserts). All gecko species had negative residual limb lengths and nearly all anoles had positive, resulting in a two-humped distribution of residual values (Fig. 3A insert). We then calculated residual limb lengths for each group separately (Fig. 3B). This approach generated normally distributed residuals for geckos (Shapiro-Wilk normality test $p = 0.5$, see Fig 3B inserts), yet the anole residuals still differed significantly from normal (Shapiro-Wilk normality test $p < 0.01$, see Fig 3B inserts), possibly due to the presence of multiple anole ecomorphs (see Fig. 4B). We examined the relationship between limb length and perch diameter, using both sets of residuals (geckos and anoles combined and separate, Fig. 4). Residual limb lengths calculated by combining anoles and geckos were positively correlated with perch diameter

(Fig. 4A, $\lambda = 1.0$, $\mathbf{p} < \mathbf{0.01}$), suggesting that, across all focal species, species with longer limbs use wider perches. Residual limb lengths calculated for each group separately suggested different patterns. Residuals of anole limb length were significantly and positively correlated with perch diameter (Fig. 4B, $\lambda = 1.0$, $\mathbf{p} < \mathbf{0.01}$), consistent with previously published observations and when we examined gecko microhabitat and gecko-specific residual limb lengths, we observed widespread microhabitat convergence with anole ecomorphs (Fig. 2). In addition, *Strophurus* geckos and grass-bush anoles both had relatively long limbs and used low, narrow perches. Conversely, when we examined residual gecko limb length and perch diameter, limb length was significantly negatively correlated with perch diameter (Fig 4C, $\lambda = 0.0$, $\mathbf{p} < \mathbf{0.02}$), suggesting gecko species with longer limbs used narrower perches, contradicting the pattern observed in anoles. Similarly, geckos with longer proximal and mid-hind and forelimb lengths used narrower perches (hind prox: $\lambda = 0.0$, $\mathbf{p} < \mathbf{0.01}$; hind mid: $\lambda = 0.0$, $\mathbf{p} < \mathbf{0.01}$; hind dist: $\lambda = 1.0$, $p = 0.8$; fore prox: $\lambda = 0.0$, $\mathbf{p} < \mathbf{0.01}$; fore mid: $\lambda = 0.0$, $\mathbf{p} = \mathbf{0.02}$; fore dist: $\lambda = 1.0$, $p = 0.8$; fore total: $\lambda = 0.2$, $\mathbf{p} = \mathbf{0.05}$).

Our second hypothesis examined limb length and perch type, predicting that arboreal geckos would have shorter limbs compared to saxicolous species, similar to patterns described for other lizard groups. Our results supported our hypothesis. Geckos observed more often on vegetation had significantly shorter residual proximal limb lengths and slightly longer distal forelimbs. Distal forelimb length was weakly positively correlated with the use of vegetation (hind prox: $\lambda = 1.0$, $\mathbf{p} = \mathbf{0.01}$, Fig. 5; hind mid: $\lambda = 0.0$, $p = 0.4$; hind dist: $\lambda = 1.0$, $p = 0.3$; hind total: $\lambda = 0.0$, $p = 0.7$; fore prox: $\lambda = 1.0$, $\mathbf{p} = \mathbf{0.03}$; fore mid: $\lambda = 1.0$, $p = 0.6$; fore dist: $\lambda = 1.0$, $p = 0.08$; fore total: $\lambda = 1.0$, $p = 0.4$).

Lastly, we examined gecko morphology and adhesive performance in relation to perch angle. Multiple limb segment lengths were negatively correlated with perch angle, i.e., gecko species with significantly longer proximal, mid, and total limb segment lengths used shallower perch angles (hind prox: $\lambda = 0.0$, $\mathbf{p} = \mathbf{0.01}$; hind mid: $\lambda = 0.0$, $\mathbf{p} = \mathbf{0.04}$; hind dist: $\lambda = 1.0$, $p = 0.8$; hind total: $\lambda = 0.0$, $\mathbf{p} = \mathbf{0.02}$, Fig. 6; fore prox: $\lambda = 0.0$, $\mathbf{p} = \mathbf{0.03}$; fore mid: $\lambda = 0.0$, $\mathbf{p} = \mathbf{0.02}$; fore dist: $\lambda = 1.0$, $p = 0.8$; fore total: $\lambda = 0.4$, $\mathbf{p} = \mathbf{0.03}$). To examine the relationship between limb length and performance, we removed one outlying species with very short limbs and a high detachment angle (*Ebenavia inunguis*). We found TAD was significantly positively correlated with residual distal fore and hindlimb length (hind prox: λ

= 1.0, $p = 0.1$; hind mid: $\lambda = 1.0$, $p = 0.8$; hind dist: $\lambda = 1.0$, $\mathbf{p} = \mathbf{0.02}$, Fig. 7; hind total: $\lambda = 1.0$, $p = 0.8$; fore prox: $\lambda = 1.0$, $p = 0.4$; fore mid: $\lambda = 1.0$, $p = 0.1$; fore dist: $\lambda = 0.9$, $\mathbf{p} = \mathbf{0.03}$; fore total: $\lambda = 1.0$, $p = 0.9$) and negatively with SVL (Fig. 8, $\lambda = 1.0$, $\mathbf{p} < \mathbf{0.01}$), suggesting that gecko species with longer hands, and feet, or both, and shorter bodies, have higher toe detachment angles.

Discussion

In this study, we evaluated relationships between gecko limb morphology, microhabitat, and adhesive performance, comparing geckos to anoles and other lizard groups to investigate the generality of previously described ecomorphological patterns. Our first hypothesis predicted that geckos would have similar ecomorphological patterns to those observed in *Draco*, *Tropidurus*, and anoles (Losos and Sinervo 1989; Losos and Irschick 1996; Kohlsdorf et al. 2001; Losos 2009; Jones and Jayne 2012; Ord and Klomp 2014), i.e., shorter-limbed species would use narrower perches. We found that arboreal geckos and anoles did use similar microhabitats (Fig. 2), and that the morphology of *Strophurus* geckos and grass-bush anoles overlapped, with both groups using narrow perches and having short limbs (Fig 4). However, when we examined the relationships between perch diameter and limb length, we observed striking differences: geckos using narrower perches had relatively longer (not shorter) limbs (Fig. 4). We first supposed this difference might have occurred because there is no gecko twig-ecomorph analog, thereby causing different overall perch diameter and limb length relationships for geckos and anoles. We then reanalyzed the relationship between anole limb lengths and perch diameter, removing twig anoles, and still observed a significant positive relationship for anoles ($\lambda = 1.0$, $\mathbf{p} < \mathbf{0.01}$;) suggesting geckos and anoles may be negotiating the trade-off between balance and speed during locomotion on narrow perches differently.

While both geckos and anoles have adhesive pads (*Draco* and *Tropidurus* lizards lack adhesive pads), geckos, as a group, have higher detachment angles than anoles (Hagey 2013), allowing geckos to transform more applied force into negative normal force. This ability may allow geckos to more firmly adhere to narrow perches, improving their stability, and possibly reducing the need to lower their center of mass via shorter limbs. Alternatively, geckos with long limbs may still lower their center of mass when on narrow perches, bringing their feet

near their bodies with acute elbow/knee angles. This kinematic approach may allow for finer foot control and placement options.

In addition to the observed divergence in the apparent influence of perch diameter on limb length of geckos and anoles, our data suggest that geckos, as a group, have shorter limbs than anoles, i.e. a lower coefficient of allometry (Gould 1971). Even after adjusting for phylogenetic non-independence in our data, geckos all had negative residuals in the overall relationship between limb length and body size, whereas the residuals of this relationship for nearly all anoles were positive (Fig. 3A). This overall difference in limb lengths between geckos and anoles can only be observed when analyzing both groups together (Fig. 3A). Conversely, combining groups may disguise other interesting relationships, as we discovered (Fig 4B, C). When we examined the relationship between limb length and perch diameter using residuals for geckos alone, we found that *Strophurus* geckos had the longest limbs relative to body length, and used the narrowest perches. While *Strophurus* may have relatively long limbs for a gecko, they may not have long limbs compared to other lizard groups. Our results illustrate that although geckos and anoles use very similar microhabitats, the two groups have evolved in divergent ways, possibly due to their unique evolutionary backgrounds, to solve the problem of locomotion on narrow perches.

We also examined the relationship between perch type and limb length. Rock-dwelling lizards often have longer limbs (Vitt et al. 1997; Goodman et al. 2008), but this is not always the case (Miles 1994; Revell et al. 2007). We found arboreal geckos had shorter limbs than terrestrial and saxicolous geckos, supporting our second hypothesis (Fig. 6), and suggesting that the use of large, flat, and vertical surfaces likely selects for longer limbs. We encourage defining microhabitats by their biomechanical requirements (how locomotion occurs on them) instead of their composition, and also considering the animal's size in relation to the features of the microhabitat to improve our understanding of the biomechanics of climbing lizards (Losos and Sinervo 1989; Sinervo and Losos 1991; Vanhooydonck and Van Damme 2001; Zaaf and Van Damme 2001; Goodman et al. 2007; Jusufi et al. 2008; Goodman et al. 2009; Losos 2009; Wang et al. 2011). Lizards may also navigate similar microhabitats using different locomotion strategies, for example, chameleons and twig anoles appear to move along the top of branches and twigs, while Lacertids “clamber” through the vegetation matrix (Peterson 1984; Vanhooydonck and Van Damme 2001; Jones and Jayne

2012). This clambering style may also describe how *Strophurus* and grass-bush anoles move through arboreal microhabitats. Future studies considering kinematics in regards to the width and complexity of perches relative to lizard sizes and movement types would greatly improve our understanding of locomotion adaptation and variability across and within species (Russell and Bels 2001).

Very few studies have examined the adhesive system of geckos in an ecological context. Based on results from studies of anole toe pad morphology and performance (Irschick et al. 1996; Losos 2009) and gecko toe pad biomechanics (Autumn et al. 2006a; Hagey et al. 2014), we hypothesized that geckos using steeper perches would have longer toes and feet (distal limb segments). Instead, we found that species using steeper perches had relatively shorter proximal, mid-, and total limb segment lengths than species using more horizontal surfaces (Fig. 6), whereas there was with no significant relationship with distal limb lengths. Shorter proximal limb lengths may bring the body closer to the surface and reduce the chance of toppling off steep perches. In addition, we found that the angle of toe detachment (TAD) in geckos was positively correlated with distal limb length (Fig. 7). Although we may have expected that species with higher detachment angles may more easily transverse steep or inverted perches; we did not find such a relationship. The lack of a relationship between TAD and perch angle, taken together with the significant relationship between TAD and distal limb length, suggests there may be subtle relationships linking limb length, perch angle, and the adhesive system (Gardner 1984; Aerts et al. 2000; Harmon et al. 2007; Losos 2009; Russell and Higham 2009; Wang et al. 2010). Padded lizards may adapt to microhabitats with concurrent and complementary changes to both their adhesive and locomotor systems. Species using steep microhabitats may have limb length adaptations that help navigate obstacles, or allow their toe pads to stick more efficiently on non-horizontal surfaces (Higham and Russell 2010). Also, terrestrial or semi-terrestrial padded species may develop longer toes, with more distal adhesive structures, to increase the toe area that can be deployed while running with their toes hyperextended (Collins et al. 2015). To investigate such patterns, it is important to consider individual limb segments in addition to total limb length, allowing a more detailed understanding of the interaction between microhabitat, the locomotor and adhesive systems.

When considering the ecomorphology of padded lizards, it is also important to consider adhesive performance. Previous studies, primarily examining anoles, have focused on shear force, pad area, and microhabitat, and have found that shear force correlates positively with pad area, and pad area correlates positively with perch height (Irschick et al. 1996; Macrini et al. 2003; Elstrott and Irschick 2004; Crandell et al. 2014). These results suggest that the absolute shear force generated by anoles likely increases traction while climbing (Losos 2009) while the role of adhesion is still unclear. We may need to consider the generation of shear and adhesion separately, as lizards may use shear and adhesive forces differently. Shear forces generated by padded lizards likely increase traction, possibly as a supplement to, or replacement for, claws on smooth surfaces (Crandell et al. 2014). Adhesion is the generation of negative normal force relative to a substrate, which is presumably useful for traversing steep surfaces or overhangs, or to prevent removal from a substrate by a predator or competitor.

We found a significant negative relationship between gecko SVL and TAD (Fig. 8). While lizard length is correlated with mass, our measure of toe detachment angle is mass independent (Autumn et al. 2006a). Thus, the negative relationship we observed suggests that larger lizards may rely less on adhesion and more on other structures, such as claws, while climbing (Crandell et al. 2014). There may also be constraints on large-bodied geckos that prevent them from relying heavily on adhesion, for example limitations on the strength of lizards' toe joints to support large body masses. Additional ecological observations focusing on the movement of large and small-bodied geckos through their environment, as well as kinematic studies of the use of the claws and adhesive toes in different-sized geckos would be informative (Russell and Johnson 2014).

Lastly, perch texture may be an important factor influencing the locomotion of different species, potentially strongly affecting the clinging abilities of padded lizards. Although much theoretical work has been done on surface texture and gecko performance (Vanhooydonck et al. 2005; Huber et al. 2007; Persson 2007; Russell and Johnson 2007; Pugno and Lepore 2008; Russell and Johnson 2014), few studies have examined shear forces and adhesion separately in regards to their relationship to texture and microhabitat use (but see Russell and Johnson 2014). We observed that rock-dwelling species (*Oedura sp.* and *O. coggeri*) had lower toe detachment angles, possibly suggesting weak selection for adhesion

in these habitats. We often observed arboreal geckos using ironbark (*Eucalyptus* spp.) and paperbark (*Melaleuca* spp.) trees. Generating adhesion and shear forces via toe pads on these surfaces would be difficult because the bark of ironbark trees is very rough, with large valleys and ridges, greatly limiting the available surface area for adherence (Russell and Johnson 2014). Conversely, the bark of paperbark trees is smooth, but dusty and flaky, again limiting a species' clinging ability and likely fouling their toe pads (see Cole et al. 2005; Hansen and Autumn 2005). Thus, the difficulties associated with using some arboreal perches may select for higher detachment angles to compensate. Future studies quantifying perch surface texture and setal morphology would be invaluable to further our understanding of evolutionary patterns and adaptations of the gecko adhesive system.

In conclusion, we investigated the generality of previously described ecomorphological patterns using geckos as a focal group, and found that geckos had similar microhabitat preferences to that of other lizards, with interesting differences. We found that arboreal geckos had shorter limbs, similar to patterns observed in skinks. *Strophurus* geckos had similar limb lengths and habitat use patterns as anole grass-bush species, yet overall, geckos showed different limb-length to perch-diameter relationships than anoles. We also observed differences in relative limb lengths of geckos and anoles, suggesting ecomorphological adaptations to similar environments may occur through different morphological changes for each group. Our results highlight the interplay between adaptation and historical contingency often occurring during the evolutionary process, and the need to consider this in studies of ecomorphology.

Acknowledgements

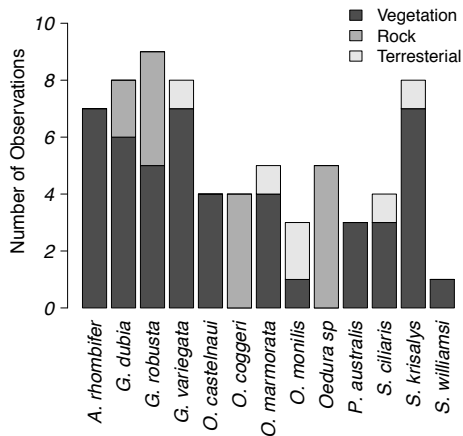
We received helpful comments from two anonymous reviewers. Our field techniques were approved by the University of Idaho animal care and use committee (protocol #2012-14), James Cook University ethics committee (JCU-A1813), and the Queensland Department of Environment and Heritage Protection (scientific collection permit #WISP11483112). We received funding from the National Geographic Society and the Waitt Institute (#W216-12) and the BEACON Center for the Study of Evolution in Action (Request #302, #429) via the University of Idaho's Institute for Bioinformatics and Evolutionary Studies (IBEST). We constructed custom field equipment with the assistance of the Autumn lab, Mitch Day, the

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Data Accessibility

Data have been accessioned into Dryad ([xx.xxxx/dryad.xxxx](#)).

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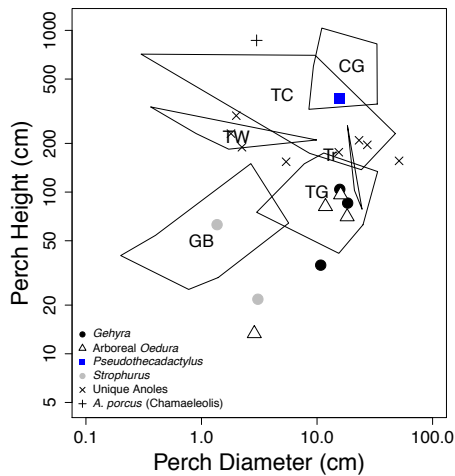


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484 Figure 1. Variation in perch type use across Queensland geckos. The number of observed
 485 individuals using vegetation (dark gray), rocks (medium gray), and the ground (light gray)
 486 are shown.

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490 Figure 2. Perch height versus perch diameters used by arboreal geckos. Polygons indicate
 491 ranges for anole ecomorphs (Losos 1990a, 1994a; Ord and Klomp 2014). Symbols are: CG =
 492 crown giant, TC = trunk-crown, TW = twig, TG = trunk ground, GB = grass bush, *Gehyra*
 493 *spp.* (black circles), *Oedura spp.* and *Amalosia rhombifer* (white triangles),
 494 *Pseudothecadactylus australis* (blue square), *Strophurus spp.* (grey circles), non-ecomorph
 495 (unique) anole species (X's), and *Anolis porcus*, from the subgenus *Chamaeleolis*, (+).

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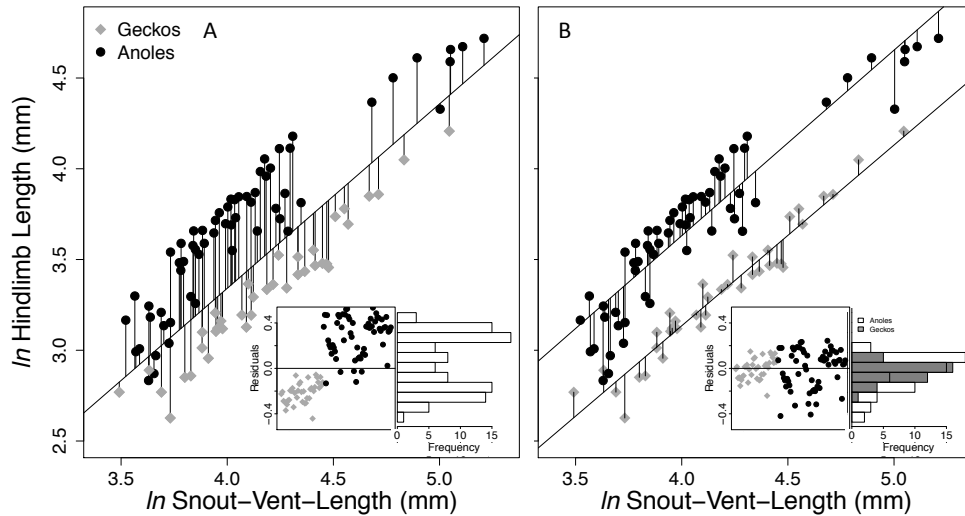


Figure 3. Body size versus hind limb lengths of geckos (grey) and anoles (black), showing (A) residuals from a single regression, and (B) residuals from separate regressions. Variation in residuals is shown in inserted scatter plots and horizontal bar graphs.

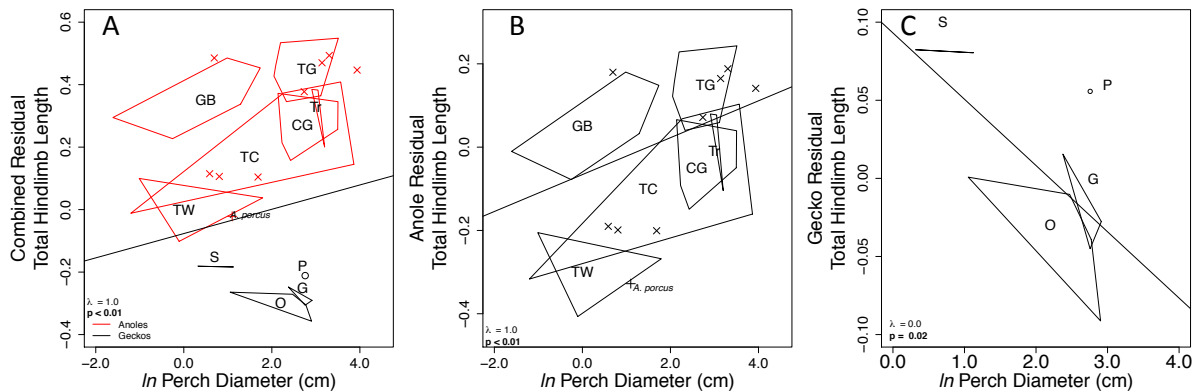


Figure 4. Relationship between residual limb length and perch diameter using among groups residuals (A) and within group residuals (B and C) All plots display PGLS correlation line, Pagel's λ , and slope p-values. Symbols are: CG = crown giant, TC = trunk-crown, TW = twig, TG = trunk ground, GB = grass bush, *Anolis porcus*, from the subgenus *Chamaeleolis* (+), *Gehyra* spp. = G, arboreal *Oedura* spp. and *Amalosia rhombifer* = O, *Pseudothecadactylus australis* = P, *Strophurus* spp. = S. Plot A: Positive correlation between

among group residuals and perch diameter. Anole non-ecomorph species and ecomorph space (red symbols and polygons), gecko genera (black polygons). Plot B. Positive correlation between limb length residuals and perch diameter for anoles. Plot C. Negative correlation between residual gecko limb length and perch diameter.

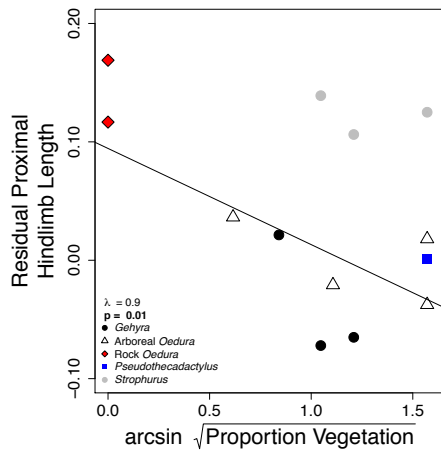


Figure 5. Negative correlation between residual proximal hind-limb lengths and the proportion of vegetation use for each species (forelimbs, not shown, showed a similar pattern). Symbols are: arboreal *Gehyra* spp. (black circles), arboreal *Oedura* spp. and *Amalosia rhombifer* (white triangles), rock-dwelling *Oedura* spp. (red diamonds), arboreal *Pseudothecadactylus australis* (blue square), and arboreal *Strophurus* spp. (grey circles). Line = PGLS model with estimated Pagel's λ and slope p-values.

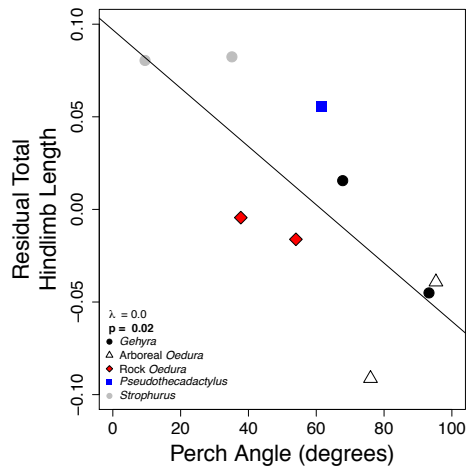


Figure 6. Negative correlation between perch angle and proximal hindlimb length (and fore-, mid-, and total residual lengths, not shown here). Symbols are: arboreal *Gehyra* spp. (black circles), arboreal *Oedura* spp. and *Amalosia rhombifer* (white triangles), rock-dwelling *Oedura* spp. (red diamonds), arboreal *Pseudothecadactylus australis* (blue square), and arboreal *Strophurus* spp. (grey circles). Line = PGLS model with estimated Pagel's λ and slope p-values.

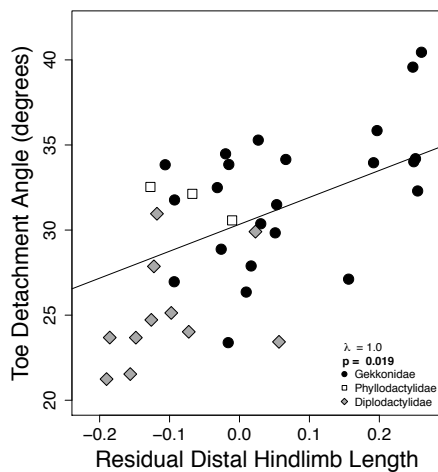


Figure 7. Correlation between gecko distal hindlimb length and toe detachment angle (a similar relationship occurs for fore limbs, not shown). Symbols are: Gekkonidae geckos (black circles), Phyllodactylidae geckos (open squares), Diplodactylidae geckos (grey diamonds). PGLS correlation line, Pagel's λ , and slope p-values are also displayed.

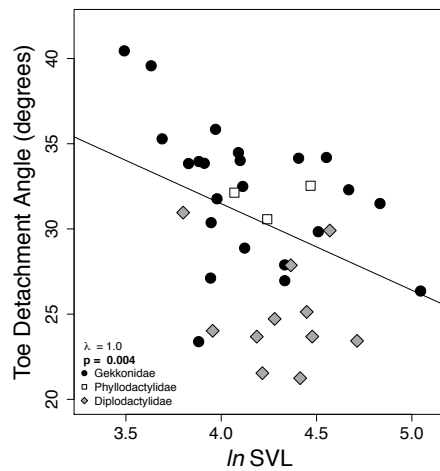


Figure 8. The negative relationship between snout-to-vent length of geckos and toe detachment angle. Symbols are: Gekkonidae geckos (black circles), Phyllodactylidae geckos (open squares), Diplodactylidae geckos (grey diamonds). PGLS correlation line, Pagel's λ , and slope p-values are also displayed.

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Microhabitat Data

Geckos

	PH	ArbPD	PercTree	PA
<i>Anolis rhombifer</i>	81.43	1182.0	1.00	NA
<i>Gehyra dubia</i>	85.50	184.1	0.75	NA
<i>Gehyra robusta</i>	35.33	10.76	0.56	67.80
<i>Gehyra variegata</i>	104.00	15.73	0.88	93.25
<i>Oedura castelnaui</i>	96.25	16.00	1.00	95.30
<i>Oedura coggeri</i>	44.50	NA	0.00	37.75
<i>Oedura marmorata</i>	70.40	18.22	0.80	76.00
<i>Oedura monilis</i>	13.33	2.86	0.33	NA
<i>Oedura sp.</i>	358.00	NA	0.00	54.00
<i>Pseudotoecadactylus australis</i>	380.00	15.76	1.00	61.50
<i>Strophurus ciliaris</i>	21.75	3.08	0.75	9.50
<i>Strophurus krisalyis</i>	62.88	1.36	0.88	35.13
<i>Strophurus williamsi</i>	NA	NA	1.00	NA

Anoles

Species	PH	ArbPD	Ecomorph
<i>Anolis ahi</i>	103.80	8.45	TC
<i>Anolis alinger</i>	462.90	18.85	TC
<i>Anolis allisoni</i>	310.30	12.05	TC
<i>Anolis allogus</i>	128.40	8.07	TC
<i>Anolis allogus_Eco</i>	88.00	4.50	TC
<i>Anolis altatus</i>	92.80	3.06	GB
<i>Anolis angusticeps</i>	309.40	0.94	TW
<i>Anolis angusticeps_Eco</i>	184.20	1.72	TW
<i>Anolis angusticeps2_Eco</i>	210.00	0.99	TW
<i>Anolis argenteus</i>	209.00	23.10	U
<i>Anolis argillaceus</i>	230.00	1.80	U
<i>Anolis bahoruensis</i>	150.00	2.68	GB
<i>Anolis baletatus</i>	100.00	14.00	CG
<i>Anolis barahonae</i>	825.00	33.00	CG
<i>Anolis bartschi</i>	296.90	2.00	U
<i>Anolis bremeri</i>	NA	NA	TG
<i>Anolis brevisirois</i>	102.50	21.07	T
<i>Anolis centralis</i>	154.00	5.40	U
<i>Anolis chlorocymus</i>	357.40	10.62	TC
<i>Anolis christophei</i>	195.00	27.23	U
<i>Anolis coelestinus</i>	252.50	20.92	TC
<i>Anolis cooki</i>	149.60	7.75	TG
<i>Anolis cristatellus</i>	118.90	13.27	TG
<i>Anolis curvieri</i>	325.00	8.50	CG
<i>Anolis cybotes</i>	142.60	24.52	TG
<i>Anolis distichus</i>	257.40	18.33	T
<i>Anolis equestris</i>	402.90	15.29	CG
<i>Anolis evermanni</i>	335.20	35.29	TC
<i>Anolis gormanii</i>	350.10	33.20	CG
<i>Anolis grahmani</i>	247.90	17.71	TC
<i>Anolis guazuma</i>	230.00	0.90	TW
<i>Anolis gundlachi</i>	133.90	33.45	TG
<i>Anolis homolechis</i>	130.70	22.45	TG
<i>Anolis homolechis_Eco</i>	75.00	3.00	TG
<i>Anolis insolitus</i>	336.30	0.36	TW
<i>Anolis islepinis</i>	713.00	0.30	TC
<i>Anolis jubae</i>	99.00	10.30	TG
<i>Anolis krugi</i>	64.30	5.68	GB
<i>Anolis lineatopus</i>	100.10	25.97	TG
<i>Anolis longitibialis</i>	133.00	9.00	TG
<i>Anolis lousiana</i>	78.50	24.50	T
<i>Anolis lucius</i>	156.00	51.27	U
<i>Anolis lateogularis</i>	563.60	11.31	CG
<i>Anolis marcanoti</i>	107.00	11.56	TG
<i>Anolis mestrei</i>	174.40	11.44	TG
<i>Anolis noblei</i>	600.00	9.30	CG
<i>Anolis occidus</i>	NA	NA	TW
<i>Anolis olsoni</i>	46.10	15.14	GB
<i>Anolis opalinus</i>	137.50	24.19	TC
<i>Anolis ophiops</i>	25.00	0.78	GB
<i>Anolis patermus</i>	NA	NA	TW
<i>Anolis porcanis</i>	89.70	3.64	GB
<i>Anolis porcanus</i>	230.00	47.65	TC
<i>Anolis porcanus_Eco</i>	173.60	8.63	TC
<i>Anolis porcus</i>	867.00	3.00	CH
<i>Anolis pulchellus</i>	29.60	1.39	GB
<i>Anolis pumilus</i>	189.40	2.24	U
<i>Anolis rejeux</i>	54.00	0.40	GB
<i>Anolis ricordi</i>	1033.30	11.00	CG
<i>Anolis sagrei</i>	41.80	15.44	TG
<i>Anolis sagrei_Eco</i>	75.00	21.90	TG
<i>Anolis sagrei2_Eco</i>	62.80	25.00	TG
<i>Anolis semilineatus</i>	NA	NA	GB
<i>Anolis singularis</i>	300.00	8.00	TC
<i>Anolis smaragdinus</i>	NA	NA	TC
<i>Anolis strahni</i>	NA	NA	TG
<i>Anolis stratus</i>	701.30	9.64	TC
<i>Anolis valencienae</i>	231.20	6.00	TW
<i>Anolis vandicae</i>	40.50	0.20	GB
<i>Anolis vermiculatus</i>	176.40	15.43	U

Geckos

Species	SVL	HTtotal	TTotal	Hprex	Hmid	Hdist	Fprex	Fmid	Fdist
<i>Afreodura havequensis</i>	38.73	33.60	25.74	11.87	11.10	10.63	1.33	9.97	7.44
<i>Afreodura liveoides</i>	53.40	22.62	16.02	8.76	7.28	6.58	5.52	5.96	4.54
<i>Anolis rhombifer</i>	44.71	17.30	13.62	6.40	5.57	5.33	4.58	5.12	3.92
<i>Dixonius siamensis</i>	48.50	26.35	14.54	7.05	6.87	6.43	4.52	5.96	4.06
<i>Ebenavia inunguis</i>	41.75	13.83	10.98	4.95	4.37	4.52	3.63	4.27	3.09
<i>Gehyra dubia</i>	59.75	22.81	19.66	7.75	7.11	7.96	6.38	6.88	6.40
<i>Gehyra mutilata</i>	49.92	19.22	14.91	6.46	6.12	6.64	4.38	5.69	4.83
<i>Gehyra oceanica</i>	11.94	34.88	26.52	11.61	11.21	12.06	7.23	9.56	9.73
<i>Gehyra robusta</i>	61.13	24.37	21.40	8.66	7.66	8.06	6.85	7.85	6.71
<i>Gehyra variegata</i>	40.00	17.44	14.51	6.43	5.46	5.56	4.67	5.46	4.38
<i>Gekko badenii</i>	40.00	17.44	14.51	6.43	5.46	5.56	4.67	5.46	4.38
<i>Gekko gecko</i>	155.38	67.18	50.15	22.87	22.11	22.20	13.28	18.51	15.37
<i>Gekko smithii</i>	125.57	57.35	44.37	19.54	19.24	18.57	13.19	16.16	18.02
<i>Hemidactylus angulatus</i>	90.83	26.93	19.80	9.97	8.78	8.18	5.92	7.87	6.01
<i>Hemidactylus frenatus</i>	51.78	22.29	17.62	8.06	7.02	7.21	5.78	6.40	5.45
<i>Hemidactylus platyrus</i>	51.63	26.68	19.80	8.74	7.79	8.15	6.14	7.19	6.47
<i>Hemidactylus tridrus</i>	76.20	28.05	23.09	10.30	10.65	9.53	6.65	10.04	6.41
<i>Lepidodactylus lugubris</i>	40.05	15.95	11.42	5.64	4.81	5.50	3.30	4.22	3.90
<i>Lygodactylus kimhowelli</i>	37.80	19.99	14.39	5.82	5.71	6.46	4.10	5.24	5.05
<i>Mniarogekko chahoua</i>	40.05	15.95	11.42	5.64	4.81	5.50	3.30	4.22	3.90
<i>Oedura castelnaui</i>	85.50	32.43	26.48	11.19	10.54	10.70	8.61	10.28	7.59
<i>Oedura coggeri</i>	72.25	28.31	22.80	10.84	8.74	8.73	8.30	8.60	5.91
<i>Oedura marmorata</i>	88.00	31.69	27.46	11.01	10.59	10.10	8.73	10.46	8.27
<i>Oedura monilis</i>	78.67	31.02	24.23	10.69	10.76	9.57	8.11	9.56	6.87
<i>Oedura sp.</i>	82.60	32.04	27.06	12.67	9.96	9.41	9.41	10.56	7.10
<i>Phelsuma lineata</i>	60.30	28.05	20.64	9.51	8.92	10.52	6.07	7.98	6.58
<i>Phelsuma lineata</i>	94.80	43.81	31.38	13.32	13.60	16.90	7.73	11.71	11.93
<i>Phelsuma laticauda</i>	53.00	23.60	17.29	7.22	7.65	8.72	5.27	6.39	5.64
<i>Phelsuma lineata</i>	65.48	18.17	17.01	7.45	6.81	7.92	4.72	6.06	6.23
<i>Phelsuma standingi</i>	106.57	46.95	37.30	13.04	14.77	15.15	10.40	13.30	13.50
<i>Phyllodactylus wirringi</i>	38.50	24.40	19.66	8.93	8.04	7.43	6.44	7.62	5.61
<i>Pseudotoecadactylus australis</i>	60.30	28.05	23.09	10.30	10.65	9.53	6.65	10.18	10.79
<i>Rhoptropella ocellata</i>	32.83	15.94	13.79	5.08	5.22	5.64	4.12	4.95	4.73
<i>Strophurus ciliaris</i>	67.75	28.87	25.13	10.55	10.41	9.92	8.31	10.44	6.37
<i>Strophurus krisalyis</i>	65.80	28.08	24.49	9.98	10.36	7.74	8.64	9.49	6.36
<i>Strophurus williamsi</i>	32.20	22.68	18.01	8.78	7.34	6.56	5.83	7.23	4.95
<i>Tarentola mauritanica</i>	69.50	33.02	10.10	13.41	11.11	9.41	6.80	8.76	7.54
<i>Thecadactylus rapicauda</i>	87.25	32.33	28.30	10.85	10.87	10.61	8.81	10.99	8.49

Geckos

Species	SVL	HTtotal
<i>Anolis ahi</i>	37.64	46.79
<i>Anolis alinger</i>	55.90	34.80
<i>Anolis allisoni</i>	37.30	45.30
<i>Anolis allogus</i>	54.75	44.25
<i>Anolis allogus_Eco</i>	NA	NA
<i>Anolis altatus</i>	35.33	27.08
<i>Anolis angusticeps</i>	41.50	20.88
<i>Anolis angusticeps_Eco</i>	NA	NA
<i>Anolis angusticeps2_Eco</i>	NA	NA
<i>Anolis argenteus</i>	52.60	43.85
<i>Anolis argillaceus</i>	50.40	23.00
<i>Anolis bahoruensis</i>	43.93	36.20
<i>Anolis baletatus</i>	NA	NA
<i>Anolis barahonae</i>	156.33	105.33
<i>Anolis bartschi</i>	73.42	61.17
<i>Anolis bremeri</i>	54.17	40.33
<i>Anolis brevisirois</i>	47.00	35.00
<i>Anolis centralis</i>	36.13	20.25
<i>Anolis chlorocymus</i>	68.67	43.89
<i>Anolis christophei</i>	46.62	38.77
<i>Anolis coelestinus</i>	71.67	47.67
<i>Anolis cooki</i>	59.86	46.85
<i>Anolis cristatellus</i>	63.80	53.77
<i>Anolis curvieri</i>	133.50	100.60
<i>Anolis cybotes</i>	66.93	54.80
<i>Anolis distichus</i>	51.27	38.33
<i>Anolis equestris</i>	156.00	98.50
<i>Anolis evermanni</i>	62.29	47.89
<i>Anolis gormanii</i>	107.90	78.80
<i>Anolis grahmani</i>	61.07	45.43
<i>Anolis guazuma</i>	38.67	17.67
<i>Anolis gundlachi</i>	65.11	57.65
<i>Anolis homolechis</i>	56.80	41.70
<i>Anolis homolechis_Eco</i>	NA	NA
<i>Anolis insolitus</i>	41.80	23.40
<i>Anolis islepinis</i>	39.00	19.50
<i>Anolis jubae</i>	55.64	40.07
<i>Anolis krugi</i>	48.60	38.88
<i>Anolis lineatopus</i>	56.55	46.65
<i>Anolis longitibialis</i>	69.80	61.00
<i>Anolis lousiana</i>	40.00	24.70
<i>Anolis lucius</i>	65.57	52.43
<i>Anolis lateogularis</i>	183.00	112.00
<i>Anolis marcanoti</i>	55.56	46.19
<i>Anolis mestrei</i>	51.64	41.07
<i>Anolis noblei</i>	165.50	107.00
<i>Anolis occidus</i>	37.70	17.00
<i>Anolis olsoni</i>	46.46	35.77
<i>Anolis opalinus</i>	47.79	34.07
<i>Anolis ophiops</i>	38.00	24.11
<i>Anolis patermus</i>	47.00	26.00
<i>Anolis porcanis</i>	43.88	31.19
<i>Anolis porcanus</i>	70.00	41.45
<i>Anolis porcanus_Eco</i>	NA	NA
<i>Anolis porcus</i>	148.83	75.83
<i>Anolis pulchellus</i>	43.57	32.53
<i>Anolis pumilus</i>	35.50	19.93
<i>Anolis rejeux</i>	33.86	23.71
<i>Anolis ricordi</i>	NA	NA
<i>Anolis sagrei</i>	49.00	36.20
<i>Anolis sagrei_Eco</i>	NA	NA
<i>Anolis semilineatus</i>	41.80	34.50
<i>Anolis singularis</i>	46.00	27.00
<i>Anolis smaragdinus</i>	62.90	38.75
<i>Anolis strahni</i>	74.33	65.33
<i>Anolis stratus</i>	44.45	32.75
<i>Anolis valencienae</i>	62.00	38.70
<i>Anolis vandicae</i>	37.75	26.63
<i>Anolis vermiculatus</i>	119.25	90.13

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Ecomorphs (TG: trunk-ground, TC: trunk-crown, T: trunk, GB: grass-bush, TW: twig, CG: crown-giant, U: unique, CH: subgenus *Chamaeleolis*), SVL: snout-vent-length, HTotal: Total hindlimb length, FTotal: Total front limb length, Hprox: proximal hindlimb length (from inside the hip joint to outside the knee joint), Hmid: mid hindlimb length (from outside the knee joint to the ankle joint), Hdsit: distal hindlimb length (from the ankle joint to the tip of longest digit), Fprox: proximal forelimb length (from the axilla to outside the elbow joint), Fmid: mid forelimb length (from outside the elbow joint to the wrist joint), Fdist: distal forelimb length (from the wrist joint to the tip of longest digit), TADMean: Toe detachment angle.

		Queensland Museum Specimen			
Species	Collection Designation	Number	Sex	Locality	
<i>Amalosia rhombifer</i>	<i>Amalosia rhombifer</i>	QMJ92081	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Amalosia rhombifer</i>	<i>Amalosia rhombifer</i>	QMJ92086	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Amalosia rhombifer</i>	<i>Amalosia rhombifer</i>	QMJ92089	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Amalosia rhombifer</i>	<i>Amalosia rhombifer</i>	QMJ92090	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Amalosia rhombifer</i>	<i>Amalosia rhombifer</i>	QMJ92092	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Amalosia rhombifer</i>	<i>Amalosia rhombifer</i>	QMJ92112	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92101	M	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92105	F	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92108	F	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92114	M	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92115	F	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92116	M	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92123	M	Winton, QLD, Australia	
<i>Gehyra variagata</i>	<i>Gehyra variagata</i>	QMJ92129	F	Winton, QLD, Australia	
<i>Gehyra dubia</i>	<i>Gehyra dubia</i>	QMJ92082	M	Magnetic Island, QLD, Australia	
<i>Gehyra dubia</i>	<i>Gehyra dubia</i>	QMJ92083	M	Magnetic Island, QLD, Australia	
<i>Gehyra dubia</i>	<i>Gehyra dubia</i>	QMJ92087	F	Magnetic Island, QLD, Australia	
<i>Gehyra dubia</i>	<i>Gehyra dubia</i>	QMJ92088	M	Magnetic Island, QLD, Australia	
<i>Gehyra dubia</i>	<i>Gehyra dubia</i>	QMJ92091	M	Magnetic Island, QLD, Australia	
<i>Gehyra robusta</i>	<i>Gehyra robusta</i>	QMJ92120	M	Winton, QLD, Australia	
<i>Oedura castelnaui</i>	<i>Oedura castelnaui</i>	QMJ92085	M	Bustard Downs, Brooklyn Station, QLD, Australia	
<i>Oedura castelnaui</i>	<i>Oedura castelnaui</i>	QMJ92094	M	Coen, Mt White, QLD, Australia	
<i>Oedura castelnaui</i>	<i>Oedura castelnaui</i>	QMJ92125	F	Coen, Mt White, QLD, Australia	
<i>Oedura coggeri</i>	<i>Oedura coggeri</i>	QMJ92097	M	Chillagoe, QLD, Australia	
<i>Oedura coggeri</i>	<i>Oedura coggeri</i>	QMJ92099	M	Chillagoe, QLD, Australia	
<i>Oedura coggeri</i>	<i>Oedura coggeri</i>	QMJ92106	F	Chillagoe, QLD, Australia	
<i>Oedura coggeri</i>	<i>Oedura coggeri</i>	QMJ92119	M	Chillagoe, QLD, Australia	
<i>Oedura marmorata</i>	<i>Oedura marmorata</i>	QMJ92102	F	Winton, QLD, Australia	
<i>Oedura marmorata</i>	<i>Oedura marmorata</i>	QMJ92109	M	Winton, QLD, Australia	
<i>Oedura marmorata</i>	<i>Oedura marmorata</i>	QMJ92118	M	Winton, QLD, Australia	
<i>Oedura marmorata</i>	<i>Oedura marmorata</i>	QMJ92127	F	Winton, QLD, Australia	
<i>Oedura marmorata</i>	<i>Oedura marmorata</i>	QMJ92128	F	Winton, QLD, Australia	
<i>Oedura monilis</i>	<i>Oedura ocellata</i>	QMJ92080	M	Magnetic Island, QLD, Australia	
<i>Oedura monilis</i>	<i>Oedura ocellata</i>	QMJ92084	M	Magnetic Island, QLD, Australia	
<i>Oedura sp</i>	<i>Oedura marmorata</i>	QMJ92095	M	Mt. Isa, QLD, Australia	
<i>Oedura sp</i>	<i>Oedura marmorata</i>	QMJ92096	F	Mt. Isa, QLD, Australia	
<i>Oedura sp</i>	<i>Oedura marmorata</i>	QMJ92107	F	Mt. Isa, QLD, Australia	
<i>Oedura sp</i>	<i>Oedura marmorata</i>	QMJ92111	M	Mt. Isa, QLD, Australia	
<i>Pseudotothecadactylus australis</i>	<i>Pseudotothecadactylus australis</i>	QMJ92117	M	Iron Range, Portland Rd, QLD, Australia	
<i>Pseudotothecadactylus australis</i>	<i>Pseudotothecadactylus australis</i>	QMJ92122	M	Iron Range, QLD, Australia	
<i>Strophurus ciliaris</i>	<i>Strophurus ciliaris</i>	QMJ92093	M	Bedourie, QLD, Australia	
<i>Strophurus ciliaris</i>	<i>Strophurus ciliaris</i>	QMJ92098	M	Bedourie, QLD, Australia	
<i>Strophurus ciliaris</i>	<i>Strophurus ciliaris</i>	QMJ92100	M	Bedourie, QLD, Australia	
<i>Strophurus ciliaris</i>	<i>Strophurus ciliaris</i>	QMJ92113	F	Bedourie, QLD, Australia	
<i>Strophurus krisalys</i>	<i>Strophurus krisalys</i>	QMJ92103	F	Winton, QLD, Australia	
<i>Strophurus krisalys</i>	<i>Strophurus krisalys</i>	QMJ92104	M	Winton, QLD, Australia	
<i>Strophurus krisalys</i>	<i>Strophurus krisalys</i>	QMJ92110	M	Winton, QLD, Australia	
<i>Strophurus krisalys</i>	<i>Strophurus krisalys</i>	QMJ92121	F	Mt. Isa, QLD, Australia	
<i>Strophurus krisalys</i>	<i>Strophurus krisalys</i>	QMJ92124	M	Mt. Isa, QLD, Australia	
<i>Strophurus krisalys</i>	<i>Strophurus krisalys</i>	QMJ92126	M	Winton, QLD, Australia	

Table S.2 Collected Museum Specimens

We accessioned 50 wild caught lizards to the Queensland Museum (DRYAD
xx.xxxx/dryad.xxxx). Please note that species names may have been changed to follow the
museum's current species designations.

Field Toe Detachment Device

Our raw toe detachment data consisted of three variables recorded over the course of each trial (acceleration in Y and Z directions and force). Our accelerometer, attached to the rotating glass surface, allowed us to determine the angle of the glass surface throughout the course of each trial by calculating the arctangent of the ratio of the two acceleration measurements perpendicular to the axis of rotation (Fig. S.1). We observed that our acceleration data were not linear. When rotating, acceleration due to gravity changed slowly when near vertical. When near horizontal, acceleration due to gravity changed quickly.

During a performance trial, the instant the lizard detaches, our force sensor recorded the corresponding change in force (Fig. S.2). We fit a three-parameter broken regression model to our force output data to pinpoint the moment the lizard detached (Fig. S.2). We estimated the y-intercept of a horizontal line fit to the force data before the lizard fell, the time point at which the lizard fell, and the y-intercept of a horizontal line fit to the force data after the lizard detached (Fig. S.2). Using our estimated time of detachment and our data of the slide angle through time (calculated from our accelerometer data), we estimated the angle of the glass at the time of detachment (Fig. S.2).

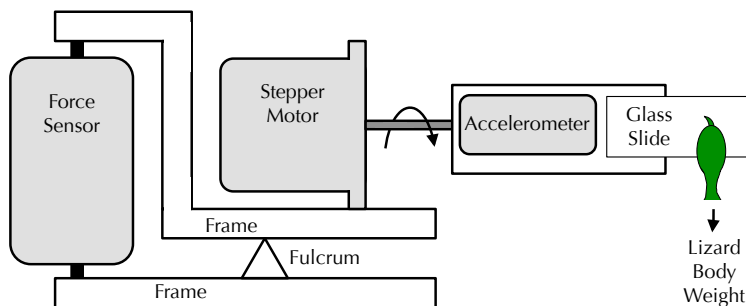


Figure S.1. Angle of Toe Detachment Field Equipment

We build a field-capable TAD device consisting of a force sensor, stepper motor, and multi-axis accelerometer. The upper frame of our apparatus acts as a lever with the fulcrum (triangle), allowing the force sensor (left side of image) to detect when a lizard detaches from the glass (right side of image). Our glass slide and accelerometer were attached to a large flat plate. The accelerometer was positioned to measure acceleration in the Y direction (currently pointing vertical in our image) and Z direction (pointing perpendicular to the mounting surface, out of the plane of the image, towards the reader).

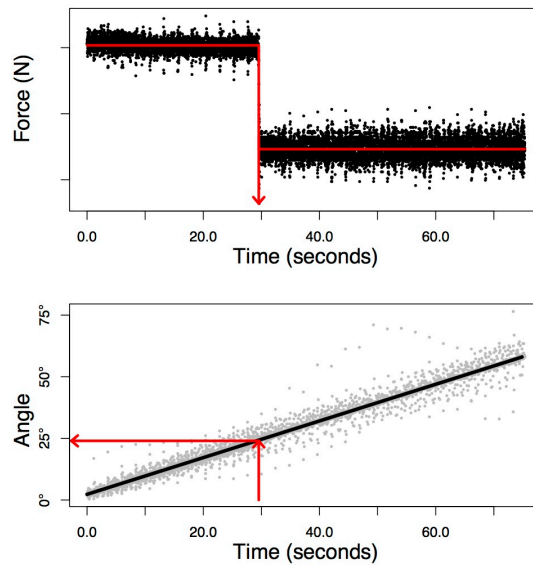


Figure S.2. Representative Toe Detachment Performance Trial

Representative data output from a single toe detachment trial is displayed. Time is on the X-axis. Raw force data (upper plot) displays our two estimated y-intercepts (red horizontal lines) and time of detachment (red vertical line, approximately 30 seconds in this example) estimated by a broken regression analysis. Raw acceleration data were used to estimate the angle of the glass slide through time (lower plot, gray points). The black line in our lower plot is the estimated glass substrate angle of the over the course of the trial. Our estimated angle of toe detachment is the point in which our estimated time of detachment intersects with our estimated angle, slightly under 25° in this example.

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